

Predatory Gastropod Drill Holes in Upper Miocene Cold Seep Bivalves, Hokkaido, Japan

KAZUTAKA AMANO

Department of Geoscience, Joetsu University of Education, Joetsu 943-8512, Japan

Abstract. Many drilled specimens of *Calyptogena pacifica* and *Conchocele bisecta* were obtained from the upper Miocene Morai Formation in western Hokkaido. Thirty-three specimens of *C. pacifica* (19.8%) and four specimens of *C. bisecta* (9.3%) were drilled. This is the first report of drilling of cold seep bivalves by either fossil or Recent predatory gastropods. The shape of the holes suggests they appear to have been drilled by the co-occurring naticids *Euspira* and *Cryptonatica*. Only two holes might have been drilled by muricids. Almost all holes were completed other than two incomplete holes. Thus, effectiveness of armor (number of incomplete holes/total number of holes) is very low (0.06).

INTRODUCTION

Chemosynthetic bivalve species of vents and seeps are eaten by bythograeid crabs, galatheid lobsters, alvinocarid shrimps, and zoarcid and bythilid fish (Van Dover, 2000). However, no gastropods feeding on these vent and seep species have been recognized. Naticids and muricids are predatory gastropods that drill their prey (Carriker, 1981; Kabat, 1990). Muricids feed mainly on ostreids, mytilids, barnacles, and carrion of fishes (Radwin & D'Attilio, 1976). Infaunal bivalves such as venerids, tellinids, and lucinids tend to be victims of naticids (Kabat, 1990). According to Kabat (1990), solemyid bivalves are not preyed upon by naticids because they live in reducing sediments. Reducing environments such as vents and seeps may preclude predation by naticids and muricids. Based on the existence of *Neomphalus*, Vermeij (1986) suggested that vents and seeps have acted as evolutionary refuges. Certainly, until now, no gastropod drill holes have been recorded from either fossil or Recent species in vent or seep communities.

Many drilled specimens of fossil *Calyptogena* and *Conchocele* were collected from the seep community of the upper Miocene Morai Formation in western Hokkaido, Japan. Here I describe these holes and discuss their ecological significance. All specimens from the Morai Formation are stored at the Joetsu University of Education (JUE).

OCCURRENCE AND PALEOBATHYMETRIC DEPTH

Fossil specimens of *Calyptogena pacifica* Dall, 1891, were described by Otatume (1942) from the upper Miocene Morai Formation in a coastal cliff section at Morai, western part of central Hokkaido (Figure 1). The Morai Formation consists of hard shale with many calcareous concretions. A shell lens (10 m wide and 30 cm thick) is

intercalated in the hard shale (Figure 2). In this bed, *Calyptogena pacifica* Dall (167 specimens) and *Conchocele bisecta* (Conrad, 1849) (43 specimens) numerically dominate the fossil community, in association with *Solemya (Acharax) tokunagai* Yokoyama, 1925 (15 specimens), taxodonts, naticids, and buccinids (Table 1). All these bivalve specimens are articulated other than 16 disarticulated specimens of *C. pacifica*. This species composition is rather similar to that of modern cold seep communities from Monterey Bay (Barry et al., 1996).

The depth ranges of the extant species overlap in the 160–200 m range (Table 1), apart from *C. pacifica* which today lives at 500–2000 m (Higo et al., 1999; Coan et al., 2000). Moreover, judging from the species diversity index ($R = (S - 1)/\log N$; R, species diversity index; S, total number of species; N, total number of individuals) and the ratio (PR/BS) of protobranchs to the total number of bivalve species, the structure of the Morai fauna ($R = 5.47$, PR/BS = 0.57) corresponds to that of modern communities living at 120–250 m depth (Amano et al., 1987; Amano & Nonaka, 2001). Therefore, the cold seep community at Morai may have lived on the lower shelf. Recently, Majima et al. (2000) described Holocene seep communities comparable to that in the Morai Formation from the lower shelf of Wakkanai, Hokkaido.

Among the mollusks from the Morai Formation, only *C. pacifica* and *C. bisecta* have gastropod drill holes. The morphology and sites of these holes are examined.

DETAILS OF DRILLED HOLES

Morphology and Site of Drilled Holes on *Calyptogena pacifica*

Among 167 specimens of *Calyptogena pacifica* (Figures 3–14), 33 specimens (19.8%) were drilled (Figures 6–12). In this paper, 16 disarticulated specimens of *C. pacifica* were calculated as individuals because these

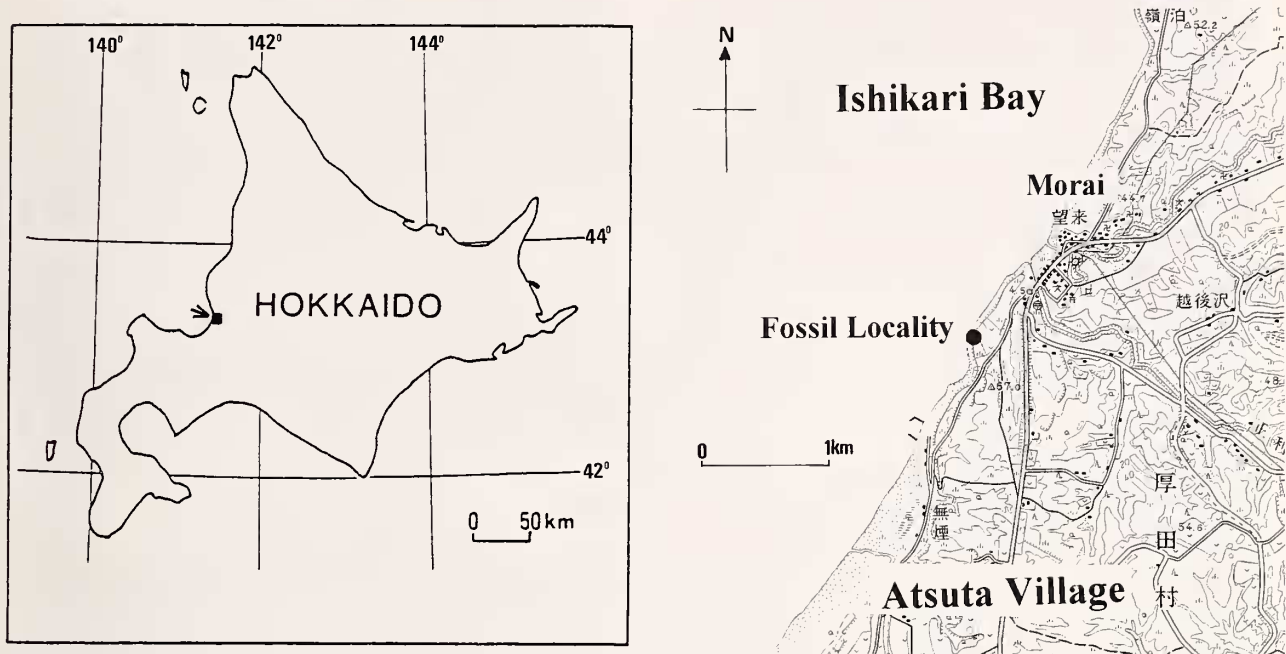


Figure 1. Fossil locality of Morai Formation (using the topographical map of "Ishikari," scale 1:50,000, published by Geographical Survey Institute of Japan).

specimens were not paired with each other, and some of the paired valves possibly broke during collection. The drilled specimens consist of 15 right valves and 18 left valves. There was no preference for right or left valves, judging from chi square test ($P = 0.05$). One right and one left valve each had an incomplete drill hole (Figure 13). There were no multiply drilled valves among these specimens. Thus, 31 of 33 holes were complete. Effectiveness of armor (number of incomplete holes/total number of holes; Vermeij et al., 1989) is very low (0.06). The outer diameter of 32 holes ranged from 1.6–4.6 mm in size. The holes are parabolic in form (inner diameter/outer diameter = 0.35–0.79; Table 2). One hole is cylindrical and small with an outer diameter of 1.3 mm (Figure 14). Except for one borehole near the posterior extremity of the right valve, most successful holes are concentrated in the upper half of the posterior part; two unsuccessful holes are situated more ventrally where the shell is thick (Figure 21).

Morphology and Site of Drilled Holes on *Conchocele bisecta*

Among 43 specimens, only two right and two left valves were drilled (Figures 15–17). All holes were complete. Two holes are present on one right and one left valve, so a total of six holes was examined. The range of outer diameters of five holes is 1.7–4.2 mm in size, with parabolic form (inner diameter/outer diameter = 0.56–

0.64; Table 3). In contrast with these holes, one drill hole is small (1.3 mm outer diameter), having a cylindrical form. Three boreholes are located at the concave part near the beak behind the flexure where the shell may be thinnest. The other three holes are located at the central and anterior parts.

DISCUSSION

Generally speaking, parabolic holes are made mainly by naticids, whereas cylindrical holes are believed to be made by muricids (Carriker & Yochelson, 1968). However, according to Kelley & Hansen (in press), naticid-like holes are made by Nassariidae, Marginellidae, and the nudibranch *Okadaia elegans*. On the other hand, muricid-like holes are drilled by octopods, buccinid *Cominella*, and Capulidae. Moreover, as pointed out by Gordillo (1994, 1998), the trophonine *Trophon geversianus* Pallas drills parabolic boreholes. However, from the Morai Formation, two small naticids were collected, *Euspira pallida* (Broderip & Sowerby, 1829) and *Cryptonatica* sp. (Figures 18, 19). Many parabolic boreholes found on *Calyplogena* and *Conchocele* from the Morai Formation were possibly drilled by these naticid species. The two cylindrical holes might have been drilled by muricids. No muricids have been found in the Morai fauna, so it is difficult to identify the possible cylindrical drill hole maker.

Calyplogena pacifica had a high frequency of drilling

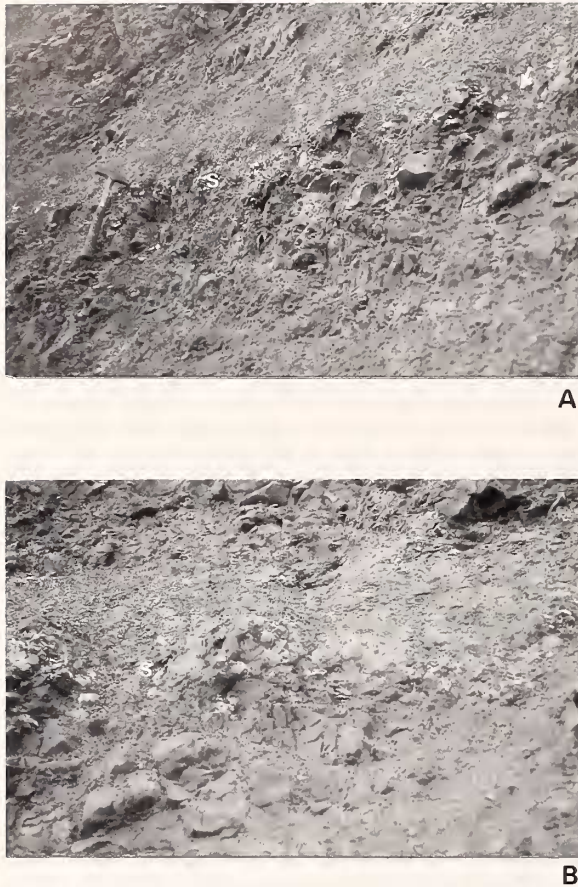


Figure 2. Occurrence of fossils. A. Shell lens (s); white arrow shows the part enlarged in B. B. Enlarged shell lens (s).

(19.8%). The living *C. pacifica* is a semi-infaunal species (Barry et al., 1996) which is susceptible to attack by predatory gastropods. Indeed, the holes of *C. pacifica* were concentrated at the upper half of shell posteriors which might be exposed above the substrata. A deep infaunal species *C. bisecta* was also drilled, whereas another deep burrower, *Solemya tokunagai* was never drilled (Figure 20). *S. tokunagai* in addition may be protected by a

Table 1

Molluscan fossils from the Morai Formation at Morai.

Species	n*	Depth (m)**
<i>Solemya (Acharax) tokunagai</i> Yokoyama, 1925	15	100–1510
<i>Acila (Acila) vigilia</i> Schenk, 1936	1	160–500
<i>A. (Truncacila) insignis</i> (Gould, 1861)	1	0–200
<i>Portlandia</i> sp.	1	
<i>Conchocele bisecta</i> (Conrad, 1849)	43	4–1400
<i>Macoma</i> sp.	1	
<i>Calyptogena pacifica</i> Dall, 1891	167	500–2000
<i>Fissidentalium</i> cf. <i>horikoshii</i> Okutani, 1982	1	
<i>Euspira pallida</i> (Broderip & Sowerby, 1829)	1	50–2433
<i>Cryptonatica</i> sp.	1	
<i>Clinopegma</i> aff. <i>borealis</i> Tiba, 1969	1	
<i>C.?</i> sp.	2	
<i>Neptunea</i> sp.	1	
<i>Buccinum</i> sp.	1	

* Number of individuals.

** After Higo et al. (1999), Coan et al. (2000).

thick periostracum like that of mytiloids (Wright & Francis, 1984; Harper & Skelton, 1993).

Drilling rates of naticids summarized by Reymont (1999) are very slow (0.01–0.025 mm/hr). At this rate, it would take a naticid about 40–100 hr to penetrate the valves (approx. 1 mm) of *Calyptogena* and *Conchocele*. Such a slow method of predation is acceptable at high latitude and in cold seeps because the drilling predators may themselves have few enemies in such environments (Aitken & Risk, 1988; Vermeij et al., 1989). The rarity of naticids and muricids in modern seeps may be due to high sulfide concentrations in the porewater. However, *C. pacifica* is known to thrive at relatively low sulfide concentrations (Barry et al., 1997). This fact and the shallow depth of the Morai seep communities may explain the presence of naticids and possibly muricids able to drill *Calyptogena* and *Conchocele* shells.

Vermeij et al. (1989) noted an equatorward decrease of incomplete drilled holes in recent mollusk shells. For example, the effectiveness is 0.06–0.61 in the cold-temperate

Figures 3–20. Bored specimens and associated species from the Morai Formation at Morai. Figures 3, 4. Dentition of *Calyptogena pacifica* Dall (JUE no. 15730-1, 2), $\times 1.5$. Figure 5. Pallial sinus of *C. pacifica* (JUE no. 15730-3), $\times 1$. Figures 6–12. Successful holes on *C. pacifica* by naticids (JUE no. 15731); Figures 6, 8, 9, $\times 1.25$; Figures 7, 12, $\times 1.3$; Figures 10, 11, $\times 1.2$. Figure 13. Unsuccessful hole on *C. pacifica* by naticids (JUE no. 15731), $\times 1$. Figure 14. Successful hole on *C. pacifica* by muricids (JUE no. 15731), $\times 1.2$. Figures 15–17. Bored holes on *Conchocele bisecta* (Conrad) (JUE no. 15732); Figure 15a. Enlarged bored holes ($\times 1.8$) in Figure 15b ($\times 0.8$), showing two failure tracks by naticids' attacks can be observed above the successful hole; Figure 16a. Dorsal view ($\times 1$) showing the bored hole by muricid; Figure 16b. Double holes by naticid (left side) and muricid (right side) ($\times 1$); Figure 17. Hole by naticid on the younger specimen ($\times 1.25$). Figure 18. *Cryptonatica* sp., JUE no. 15733, $\times 1.2$. Figure 19. *Euspira pallida* (Broderip and Sowerby), JUE no. 15734, $\times 1.2$. Figure 20. *Solemya (Acharax) tokunagai* Yokoyama, JUE no. 15735, $\times 1$.

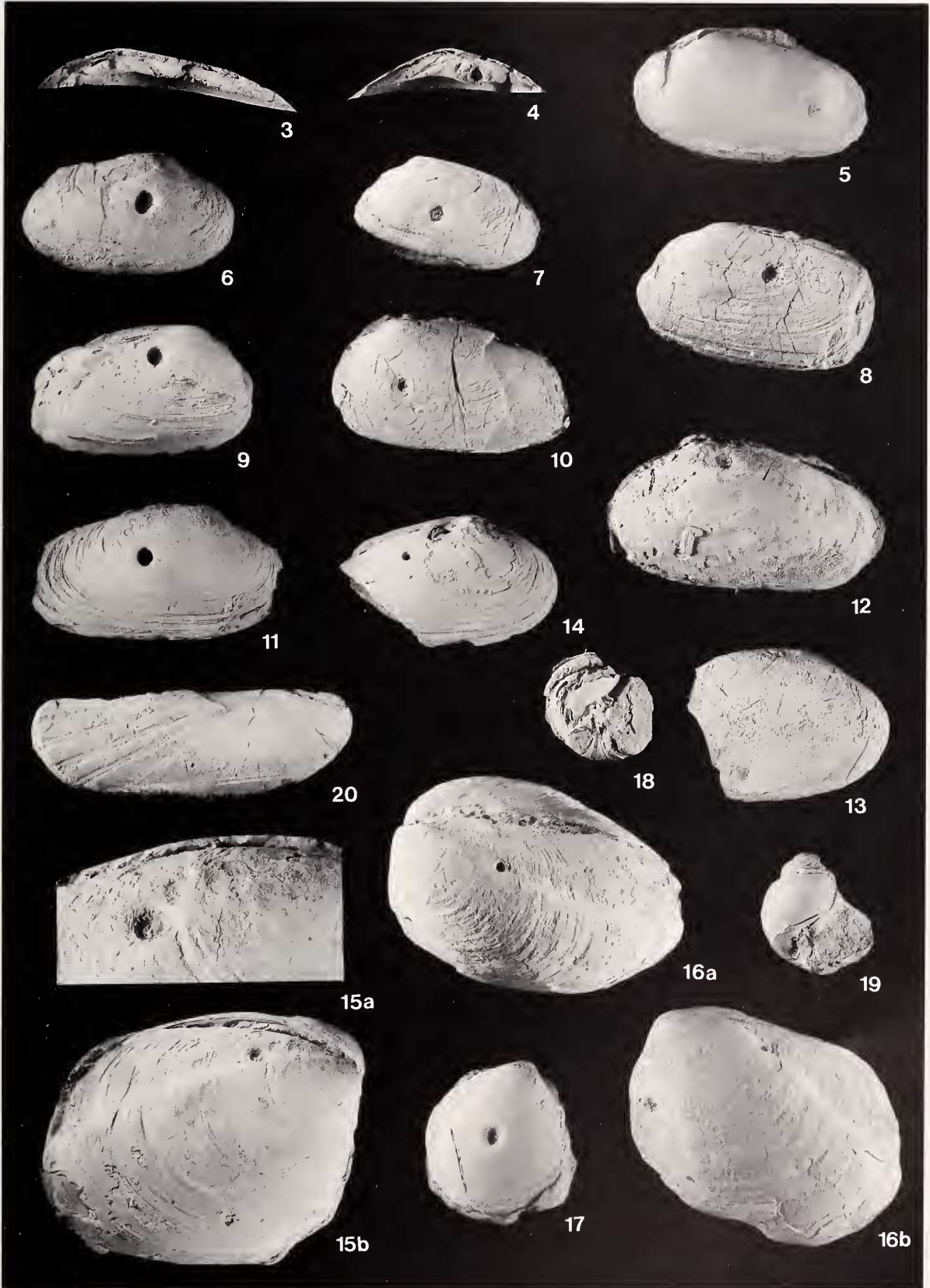


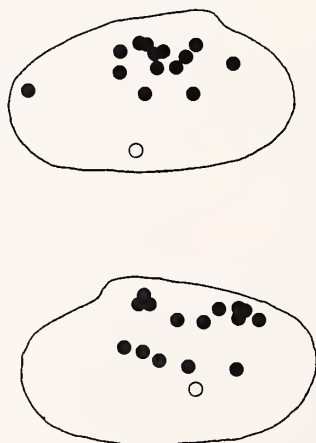
Table 2
Measurements of the holes on *Calyptogena pacifica*.

Number of specimens	L (mm)*	OD (mm)**	ID (mm)***	ID/OD
Right valve				
JUE no. 15731-R1	36.1	3.0	1.9	0.63
JUE no. 15731-R2		3.5	2.0	0.57
JUE no. 15731-R3	29.4+	2.0	0.7	0.35
JUE no. 15731-R4	26.2	2.8		
JUE no. 15731-R5		2.9		
JUE no. 15731-R6			2.4	
JUE no. 15731-R7			1.3	
JUE no. 15731-R8	43.2	2.9	2.3	0.79
JUE no. 15731-R9	33.2	3.4	2.1	0.62
JUE no. 15731-R10	35.3	2.5	1.9	0.76
JUE no. 15731-R11		4.6		
JUE no. 15731-R12	29.2	2.7	1.4	0.52
JUE no. 15731-R13	28.8	3.6	2.4	0.67
JUE no. 15731-R14		3.3	1.7	0.52
JUE no. 15731-R15		1.3	1.2	0.92
Left valve				
JUE no. 15731-L1	38.3	4.0	2.2	0.55
JUE no. 15731-L2	38.7	2.8	1.6	0.57
JUE no. 15731-L3	35.8	3.7	2.6	0.70
JUE no. 15731-L4	32.4+	3.4	1.7	0.50
JUE no. 15731-L5	31.1	3.7	2.0	0.54
JUE no. 15731-L6	25.7	2.5	1.4	0.40
JUE no. 15731-L7	28.9+	3.1	1.6	0.52
JUE no. 15731-L8	34.3+		2.7	
JUE no. 15731-L9		1.6		
JUE no. 15731-L10		2.3		
JUE no. 15731-L11			2.5	
JUE no. 15731-L12	37.7	2.8	1.0	0.36
JUE no. 15731-L13	34.2+	2.5	1.2	0.48
JUE no. 15731-L14	29.1+	3.0	1.4	0.47
JUE no. 15731-L15	28.5	2.6	1.6	0.62
JUE no. 15731-L16		2.2	1.4	0.64
JUE no. 15731-L17			1.7	
JUE no. 15731-L18	31.5	3.2	1.5	0.47

* Shell Length.

** Outer Diameter.

*** Inner Diameter.



water of Hokkaido while it is difficult to find any incomplete drillholes in the tropical area. Hansen & Kelley (1995) also found the same equatorward decrease in the Eocene molluscan fauna from the Atlantic coast of North America. When they examined the drillholes by the predatory gastropods from the upper Cretaceous to the lower Oligocene shallow deposits within the Atlantic and Gulf Coastal Plain, Kelly & Hansen (1993) showed 0.06 to 1.0 as the effectiveness of armor. They also documented an increase in effectiveness of armor through time, which they considered

←

Figure 21. Drilled sites of *Calyptogena pacifica*. Black circles are successful holes and white circles are unsuccessful holes.

Table 3
Measurements of the holes on *Conchocele bisecta*.

Number of specimens	L (mm)*	OD (mm)**	ID (mm)***	ID/OD
Right valve				
JUE no. 15732-R1	57.1	4.2	2.7	0.64
JUE no. 15732-R2	18.6	2.7	1.7	0.63
Left valve				
JUE no. 15732-L1	47.8	3.1	1.8	0.58
JUE no. 15732-L1	47.8		1.6	
JUE no. 15732-L2	41.0+	3.2	1.8	0.56
JUE no. 15732-L2	41.0+	1.3	1.2	0.92

* Shell Length.

** Outer Diameter.

*** Inner Diameter.

to be the result of escalation (Vermeij, 1987). However, Kelley et al. (2001) recognized a low rate of incompleteness of holes in the Neogene fauna. Compared to other species, *Calyplogena pacifica* from the Morai Formation has low effectiveness (0.06).

Acknowledgments. I am very grateful to Prof. G. J. Vermeij (University of California at Davis) and Dr. C. T. S. Little (University of Leeds) for their critical reading of this manuscript. I also thank Prof. P. H. Kelley (University of North Carolina at Wilmington) and T. Naganuma (Hiroshima University) for their information on bioerosion in fossil and Recent seep communities.

LITERATURE CITED

- AITKEN, A. E. & M. J. RISK. 1988. Biotic interactions revealed by macroborings in Arctic bivalve molluscs. *Lethaia* 21: 339–350.
- AMANO, K., S. KANNO, A. ICHIKAWA & Y. YANAGISAWA. 1987. Molluscan fauna from the Tanihama Formation in the western part of Joetsu City. Studies on the molluscan fossils from the western part of Joetsu district, Niigata Prefecture (Part 2). *Bulletin of Joetsu University of Education* 6:157–170. [in Japanese with English abstract]
- AMANO, K. & T. NONAKA. 2001. A method for estimating paleobathymetric depth from molluscan community structure. A case study in the Miocene Mizunami Group in central Japan. *Fossils (Palaeontological Society of Japan)* 70:23–34. [in Japanese with English abstract]
- BARRY, J. P., H. G. GREEN, D. L. ORANGE, C. H. BAXTER, B. H. ROBINSON, R. E. KOICHEVAR, J. W. NYBAKKEN, D. L. REED & C. M. MCHUGH. 1996. Biologic and geologic characteristics of cold seeps in Monterey Bay. *California. Deep-Sea Research (I)* 43:1739–1762.
- BARRY, J. P., R. E. KOICHEVAR & C. H. BAXTER. 1997. The influence of pore-water chemistry and physiology on the distribution of vesicomyid clams at cold seeps in Monterey Bay: implications for patterns of chemosynthetic community organization. *Limnology and Oceanography* 42:318–328.
- CARRIKER, M. R. 1981. Shell penetration and feeding by naticacean and muricacean predatory gastropods: Synthesis. *Malacologia* 20:403–422.
- CARRIKER, M. R. & E. L. YOCHELSON. 1968. Recent gastropod boreholes and Ordovician cylindrical borings. *U.S. Geological Survey Professional Paper* 593-B:1–26.
- COAN, E. V., P. V. SCOTT & F. R. BERNARD. 2000. Bivalve Shells of Western North America. Marine Bivalve Mollusks from Arctic Alaska to Baja California. Santa Barbara Museum of Natural History: Santa Barbara. 764 pp.
- GORDILLO, S. 1994. Perforaciones en bivalvos subfósiles y actuales del Canal Beagle, Tierra del Fuego. *Ameghiniana (Rev. Asoc. Paleontol. Argent.)* 31:177–185.
- GORDILLO, S. 1998. Trophonic gastropod predation on recent bivalves from Magellanic Region. Pp. 251–254 in P. A. Johnston and J. W. Haggart (eds.), *Bivalves: An Eon of Evolution*. University of Calgary Press: Calgary.
- HANSEN, T. A. & P. H. KELLEY. 1995. Spatial variation of naticid gastropod predation in the Eocene of North America. *Palaios* 10:268–278.
- HARPER, E. M. & P. W. SKELTON. 1993. A defensive value for the thickened periostracum of the Mytiloidea. *The Veliger* 36:36–42.
- HIGO, S., P. CALLOMON & Y. GOTO. 1999. Catalogue and Bibliography of the Marine Shell-Bearing Mollusca of Japan. *Elle Scientific Publications*: Yao. 749 pp.
- KABAT, A. R. 1990. Predatory ecology of naticid gastropods with a review of shell boring predation. *Malacologia* 32:155–193.
- KELLEY, P. H. & T. A. HANSEN. 1993. Evolution of the naticid gastropod predator-prey system: an evaluation of the hypothesis of escalation. *Palaios* 8:358–375.
- KELLEY, P. H., T. A. HANSEN, S. E. GRAHAM & A. G. HUNTOON. 2001. Temporal patterns in the efficiency of naticid gastropod predators during the Cretaceous and Cenozoic of the United States Coastal Plain. *Palaeogeography, Palaeoclimatology, Palaeoecology* 166:165–176.
- KELLEY, P. H. & T. A. HANSEN. In press. The fossil record of drilling predation on Bivalves and gastropods. In P. H. Kelley, M. Kowalewski & T. A. Hansen (eds.), *Predator-Prey Interactions in the Fossil Record*, Volume XX of *Topics in Geobiology*. Kluwer Academic/Plenum Publishers: New York.
- MAJIMA, R., K. KATO, H. WADA & T. MIYAUCHI. 2000. Chemosynthetic community from off Wakkanai. *Monthly Kaiyo, Extra*. 29:146–154. [in Japanese].
- OTATUME, K. 1942. On the occurrence of fossil *Calyplogena* from the Ishikari Oil-Field, Hokkaido. *Journal of the Geological Society of Japan* 49:435–437.
- RADWIN, G. E. & A. D'ATTILIO. 1976. *Murex Shells of the World*. Stanford University Press: Stanford. 284 pp.
- REYMENT, R. A. 1999. Drilling gastropods. Pp. 197–204 in E.

- Savazzi (ed.), *Functional Morphology of Invertebrate Skeleton*. John Wiley & Sons: Chichester/New York/Weinheim/Brisbane/Singapore/Toronto. 706 pp.
- VAN DOVER, C. L. 2000. *The Ecology of Deep-Sea Hydrothermal Vents*. Princeton University Press: Princeton. 424 pp.
- VERMEIJ, G. J. 1986. Survival during biotic crises: The properties and evolutionary significance of refuges. Pp. 231–246 in D. K. Elliott (ed.), *Dynamics of Extinction*. John Wiley & Sons: New York/Chichester/Brisbane/Toronto/Singapore.
- VERMEIJ, G. J. 1987. *Evolution and Escalation: An Ecological History of Life*. Princeton University Press: Princeton. 527 pp.
- VERMEIJ, G. J., E. C. DUDLEY & E. ZIPSER. 1989. Successful and unsuccessful drilling predation in recent pelecypods. *The Veliger* 32:266–273.
- WRIGHT, M. M. & L. FRANCIS. 1984. Predator deterrence by flexible shell extensions of the horse mussel *Modiolus modiolus*. *The Veliger* 27:140–142.